

## SCALING IN SENSITIVITY ANALYSIS

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**Abstract.** Population matrix models allow sets of demographic parameters to be summarized by a single value  $\lambda$ , the finite rate of population increase. The consequences of change in individual demographic parameters are naturally measured by the corresponding changes in  $\lambda$ ; sensitivity analyses compare demographic parameters on the basis of these changes. These comparisons are complicated by issues of scale. Elasticity analysis attempts to deal with issues of scale by comparing the effects of proportional changes in demographic parameters, but leads to inconsistencies in evaluating demographic rates. We discuss this and other problems of scaling in sensitivity analysis, and suggest a simple criterion for choosing appropriate scales. We apply our suggestions to data for the killer whale, *Orcinus orca*.

**Key words:** management decisions, prospective analyses for; *Orcinus orca*; parameter transformations; population matrix models; sensitivity analysis.

### INTRODUCTION

Population matrix modeling has gained acceptance and popularity with increasing applications in wildlife management and conservation biology (Crouse et al. 1987, Doak et al. 1994, Kareiva et al. 2000, Caswell 2001) and as a tool for basic ecological research (Benton and Grant 1996, Gaillard et al. 1998, Pfister 1998). Much of the focus of population matrix modeling is on the relation of demographic parameters to population change, as measured by finite rate of population increase ( $\lambda$ ) and other descriptors (Caswell 2001). In particular, sensitivity analyses address the population effects of changes in specific demographic parameters.

The sensitivity of the rate of population increase to a demographic parameter  $\theta$  is defined as the incremental rate of change in  $\lambda$  due to incremental changes in  $\theta$ :

$$\text{Sensitivity}(\lambda, \theta) = \frac{\partial \lambda}{\partial \theta}.$$

Comparisons of sensitivities for various demographic parameters are complicated by issues of scale: an absolute change of 0.10 in a survival rate can hardly be compared to an absolute change of 0.10 in fecundity. For the purpose of comparison, it seems much more reasonable to describe the effects of *proportional* changes in demographic parameters. Thus, rankings are typically based on elasticities, defined by

$$\text{Elasticity}(\lambda, \theta) = \frac{\partial \log(\lambda)}{\partial \log(\theta)}.$$

Sensitivity and elasticity are related by

$$\begin{aligned} \text{Elasticity}(\lambda, \theta) &= \frac{\partial \log(\lambda)}{\partial \log(\theta)} = \frac{\theta}{\lambda} \frac{\partial \lambda}{\partial \theta} \\ &= \frac{\theta}{\lambda} \text{Sensitivity}(\lambda, \theta) \end{aligned}$$

making explicit the interpretation of elasticity as the incremental rate of *proportional* change in  $\lambda$  related to an incremental rate of *proportional* change in  $\theta$ .

Elasticity has been widely used to evaluate the relative importance of population projection matrix cell entries and lower-level parameters; it has been used to classify life-history strategies (Heppell et al. 2000, Saether and Bakke 2000) and to determine which aspects of a species' life cycle should be targeted for management action (loggerhead turtle, *Caretta caretta*, Crouse et al. 1987; killer whale, *Orcinus orca*, Brault and Caswell 1993; Greater Prairie Chicken, *Tympanuchus cupido*, Wisdom and Mills 1997).

The appealing feature of elasticity as a metric for comparing the importance of demographic parameters is that proportional changes are unitless. It certainly does not make sense to compare absolute changes in demographic parameters measured on distinct scales, but it makes sense to compare the effects of proportional changes—or does it?

As a motivating example we focus on the population modeling of killer whales by Olesiuk et al. (1990) and Brault and Caswell (1993). The population models constructed by the two teams of researchers were similar, except for what one would hope would be an inconsequential difference of parameterization: Olesiuk et al. (1990) analyzed their model with emphasis on mortality rates, while Brault and Caswell (1993) emphasized survival rates. Since survival is  $1 - \text{mortality}$ , sensitivities to survival and mortality are of the same magnitude, only of different sign. This is sensible, and fitting: an incremental increase in survival is equal to

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an incremental decrease in mortality. The relation between elasticities of survival,  $S$ , and mortality,  $1 - S$ , is less appealing:

$$\frac{\partial \log \lambda}{\partial \log S} = - \left( \frac{S}{1 - S} \right) \frac{\partial \log \lambda}{\partial \log(1 - S)}. \quad (1)$$

Thus, elasticities for survival and mortality will be of differing magnitude unless  $S = 0.5$ . The potential for inconsistent conclusions based on elasticities of survival and mortality was noted by Hunter et al. (2000) in modeling life histories of Short-tailed Shearwaters (*Puffinus tenuirostris*). Indeed, whenever  $S > 0.5$  we will be led to believe that survival rates are more critical to the species life history than the (surely equivalent) complementary mortality rates.

In their analyses of killer whale populations, Olesiuk et al. (1990) came to the conclusion that  $\lambda$  was more sensitive to changes in reproductive parameters than changes in mortality. Brault and Caswell (1993) came to the (apparently contradictory) conclusion that  $\lambda$  was more sensitive to changes in survival than in fertility. Brault and Caswell (1993:1452) address the apparent contradiction, beginning with the following tongue-in-cheek commentary: "Both conclusions are correct analytically, but which is relevant biologically? It is perhaps an open question whether mortality or survival is more biologically fundamental. Optimists and pessimists may disagree on the matter." However, they then argue that since survival rates are high, the smallest proportional change in survival observable (due to a single death, or additional survivor) is smaller than the corresponding smallest proportional change in mortality observable, concluding that "if the purpose of the analysis is to shed light on the results of small but detectable perturbations, the survival elasticities are the most relevant."

We question this conclusion on several grounds. First, sensitivities and elasticities are defined on the basis of infinitesimal change, using derivatives, and without any consideration of whether changes are detectable (which depends on population size). Sensitivity and elasticity are functions of parameters, and not of estimates of parameters.

Second, it can be shown that the "smallest detectable [proportional] change in survival" is of smaller magnitude than the corresponding change in mortality if and only if  $S > 0.5$ . We question whether it is appropriate to label a demographic rate as more biologically relevant than its complement, solely on the basis of whether the rate exceeds 0.5.

Indeed, Eq. 1 shows that  $S > 0.5$  if and only if the magnitude of survival's elasticity is greater than that of the complementary rate; thus it is impossible for the "more relevant" rate (defined on the basis of "smallest detectable change") to have smaller elasticity.

Finally, and most fundamentally, we suggest that an objective ranking of the importance of demographic

parameters ought to place equal ranks on complementary rates.

The observation that demographic parameters are measured on different scales, which motivates the use of elasticity for ranking, ought actually to suggest that different scalings are appropriate for different types of demographic parameters—one size does not fit all. Objective rankings of the importance of demographic parameters should be based on the sensitivity of  $\lambda$  to changes in  $q(\theta)$ , where the transformation  $q(\theta)$  is appropriately chosen for specific features of the demographic parameter  $\theta$  and the purposes of the comparison. In this paper we propose a simple criterion for choosing appropriate transformations of demographic parameters. In certain cases, the log-transformation associated with elasticity is appropriate; for demographic parameters that are probabilities, our criteria point to other transformations. These have the desirable property of placing equal ranks on the importance of complementary rates.

#### TRANSFORMATIONS OF DEMOGRAPHIC PARAMETERS

Any demographic model, with fixed parameter values, can be equivalently and indistinguishably described by infinitely many reparameterized models, with the parameter values appropriately transformed. It hardly matters whether one reports that a non-negative parameter  $\theta = 2/3$ , or whether one reports that  $\theta^2 = 4/9$ .

Also, for a fixed value of  $\theta$ , it matters little whether one reports the sensitivity of  $\theta$  or of any invertible transformation  $q(\theta)$ ; the information content is the same, one can be calculated from the other. Thus if  $\theta = 2/3$  and  $\text{Sensitivity}(\log \lambda, \theta) = 0.4$ , straightforward application of the chain rule allows the conclusion that  $\text{Sensitivity}(\log \lambda, \theta^2) = 0.3$ .

For the purposes of calculation, any parameterization will do; all are equivalent. Where the choice of parameterization matters is in the interpretation of sensitivity. Sensitivity being intended as a measure of effects attributable to changes in demographic parameters, it is relevant to ask which scales are appropriate for describing such changes. Thus, for instance, elasticity describes the effects on the proportional scale, doing so by reparameterizing with  $\alpha = \log(\theta)$ . This reparameterization is reasonable for some demographic parameters, but, as we have seen, leads to distressing consequences for complementary rates. We suggest that the choice be guided by consideration of the demographic parameter as a random variable, varying through time or space, among populations or species. Then, it is reasonable to choose a scale on which the variation of the parameter is independent of its mean; under such a parameterization, the absolute magnitude of a change has meaning independent of the value of the parameter.

Such parameterizations are attainable, at least to the order of approximation of a first-order Taylor series.

Suppose that the mean value of  $\theta$  is  $\mu$ , and that the variance of  $\theta$  is related to the mean by  $\text{Var}(\theta) = f(\mu)$ . Then the delta-method approximation of the variance for the transformed parameter  $q(\theta)$  is

$$\text{Var}(q(\theta)) \approx [q'(\mu)]^2 \text{Var}(\theta) = [q'(\mu)]^2 f(\mu). \quad (2)$$

The transformation  $q(\cdot)$  is referred to as a “variance-stabilizing transformation” if  $[q'(\mu)]^2 f(\mu)$  is a constant, independent of  $\mu$ .

Fecundities, for instance, are typically more variable for  $r$ -selected animals than for  $K$ -selected animals, suggesting a relation such as  $\text{SD}(\theta) = k\mu$ , where  $\mu = E(\theta)$ , and  $k$  is a proportionality constant. Thus  $f(\mu) = k^2\mu^2$ . Setting  $q(\mu) = \ln(\mu)$  in Eq. 2, we find that  $\text{Var}(\ln(\theta)) \approx k^2$ , regardless of the value of  $\mu$ ; the logarithm transforms the demographic parameter to a scale on which changes are described independent of the mean.

We define a variance-stabilized sensitivity (VSS) for a parameter  $\theta$  by

$$\text{VSS}_q(\lambda, \theta) = \text{Sensitivity}(\log \lambda, q(\theta)) \quad (3)$$

where  $q(\cdot)$  is a variance-stabilizing transformation for  $\theta$ . The choice of evaluating sensitivity using  $\log(\lambda)$  or  $\lambda$  being inconsequential, we have chosen our definition for consistency with the definition of elasticity. The foregoing discussion shows that for parameters with distributions naturally described by mean and coefficient of variation ( $k$ ), the elasticity is a variance-stabilized sensitivity. For computation, we note that

$$\text{VSS}_q(\lambda, \theta) = \frac{\partial \lambda}{\partial \theta} \frac{1}{\lambda q'(\theta)}. \quad (4)$$

#### RETROSPECTIVE ANALYSIS, PROSPECTIVE ANALYSIS, AND SCALING

Caswell (1997, 2000) provides a useful distinction between what he terms “prospective” and “retrospective” demographic-perturbation analysis. The distinction might also be described as “functional” vs. “stochastic” analysis.

The prospective analysis asks questions about the *functional* dependence of  $\lambda$  on  $\theta$ . The questions are of a purely mathematical nature: “If  $\theta$  is changed by this much, how will  $\lambda$  be changed?” The question can be asked without regard to whether such changes are biologically reasonable. Sensitivity and elasticity are answers to specific prospective questions.

Retrospective analyses ask questions about *stochastic* relations between  $\lambda$  and  $\theta$ : “Given the functional dependence of  $\lambda$  on  $\theta$ , and given a stochastic model for  $\theta$ , how is the variation in  $\theta$  reflected in variation in  $\lambda$ ?” Caswell (1997, 2000) emphasizes historical patterns of variation in his definition of retrospective analysis; one could, however, carry out an analysis of stochastic relations between  $\lambda$  and  $\theta$  under a postulated future stochastic model for  $\theta$ .

Management actions typically are directed toward changes in  $\lambda$  rather than toward changes in  $\text{Var}(\lambda)$ . In

such cases functional (prospective) analyses are adequate and appropriate; indeed, “an observed pattern of variation [says nothing] about the effect of future changes in the vital rates.” (Caswell 2000:622). If management goals are to bring about changes in  $\text{Var}(\lambda)$  (without regard to changes in the mean value of  $\lambda$ ), then stochastic (retrospective) modeling has a role to play; however, such applications require and are conditional on postulated models for the stochastic behavior of  $\theta$ .

This distinction notwithstanding, the choice of scaling for sensitivity analyses may be reasonably guided by thinking about mean–variance relations, even for prospective analysis. Scaling (more precisely, parameter transformation) is done so that changes in parameters are comparable. Typically, the usefulness of such transformations is motivated by a desire to compare changes in qualitatively different demographic parameters (e.g., survival rates and fecundities); however, transformations are also useful for comparing changes in similar demographic parameters. An increase of 10% (proportional or absolute) is one thing for a survival rate of 50%, quite a different thing for a survival rate of 90%, and an impossibility for a survival rate of 95%. While prospective analyses need not ask questions that are biologically reasonable, managers might be less interested in asking “What if pigs could fly?” (Caswell 2001:277). The relation between parameter values and realizable magnitudes of changes, and the relation between mean and attainable variance of random variables are similar: both are subject to similar constraints.

We are not advocating the use of specific historical values of the variance of demographic parameters in defining scaled sensitivity; our definition is based on postulated mean–variance functional relations. We mention this because of a superficial similarity between variance-stabilized sensitivity (VSS) and the quantity Ehrlén and Van Groenendaal (1998) designated LTRE (from “life table response experiment”), viz.,

$$\text{LTRE}(\theta) = \text{Sensitivity}(\theta) \times \text{SD}(\theta).$$

The similarity is observed by noting, from Eq. 2, that if  $\theta$  has mean  $\mu$  and variance  $\text{Var}(\theta) = f(\mu)$ , the transformation  $q(\cdot)$  satisfying  $1/q'(\mu) = \sqrt{f(\mu)}$  is variance stabilizing. Then, substituting  $1/q'(\theta) = \sqrt{\text{Var}(\theta)}$  in Eq. 4 yields

$$\text{VSS}_q(\lambda, \theta) = \text{Sensitivity}(\theta, \lambda) \frac{\text{SD}(\theta)}{\lambda}.$$

The difference is that in Ehrlén and Van Groenendaal’s (1998) development,  $\text{SD}(\theta)$  is a constant (historical value), whereas in our development,  $\text{SD}(\theta)$  is a function relating the variability and expected value of  $\theta$ . VSS provides an alternative scaling to elasticity, and is defined for prospective analysis, rather than inferences about the variability in  $\lambda$ .

Tempting as it may be to duck the issue of scaling, one cannot: even if one chooses to evaluate sensitivity

on the "original scale" (whatever that may mean), one has chosen a scale. It is desirable that our understanding of the size of a change should be independent of the actual value of the parameter; this goal is accomplished, at least approximately, through the use of variance-stabilizing transformations. In the next section, we apply this reasoning to choosing a scale for demographic parameters that are probabilities (e.g., survival rates and transition probabilities), and hence bounded by 0 and 1.

#### VARIANCE-STABILIZING TRANSFORMATIONS FOR PROBABILITIES

Families of random variables distributed on  $[0, 1]$  are not naturally described by their means and variances, nor by their means and coefficients of variation; the ranges of possible values for variance and coefficient of variation depend on the mean. A variance of 0.21 is possible, but only if the mean is in the range (0.30, 0.70); a coefficient of variation of 0.5 is possible, but only if the mean is  $<0.80$ . These restrictions on the feasible combinations of mean and variance arise from the identity

$$0 \leq \text{Var}(X) \leq \mu(1 - \mu) \quad (5)$$

for random variables  $X$ , distributed on  $[0, 1]$ , with mean  $\mu$  (see Appendix). The identity (Expression 5) can be re-expressed as

$$\text{Var}(X) = A\mu(1 - \mu) \quad (6)$$

where  $0 \leq A \leq 1$ . The value of  $A$  is not constrained by the mean; it is a natural descriptor of the variability of  $X$ , representing the proportion  $\text{Var}(X)$  is of the maximum value attainable, given the mean  $\mu$ . It is instructive to recall the familiar formula for the variance of a sample proportion, viz.,  $\text{Var}(\hat{p}) = p(1 - p)/n$ , where  $p$  is the population proportion and  $n$  is the sample size; the parameter  $A$  in Eq. 6 is inversely related to the sample size for this random variable.

Letting,  $f(\mu) = A\mu(1 - \mu)$ ,  $q(\mu) = \sin^{-1}(\sqrt{\mu})$  is found to be a variance-stabilizing transformation for random variables with mean-variance relation given by Eq. 6. Using Eq. 2, we find that  $\text{Var}(q(X)) \approx A/4$ . This arcsine square-root transformation may be familiar for its use in analyses of proportions; in that context, the reparameterization allows better approximation by models in which means and variances are functionally independent.

Demographic parameters that are probabilities (such as survival and transition rates) are likely to be appropriately modeled as satisfying Eq. 6. The resulting variance-stabilized sensitivity (VSS) metric has the pleasing property that

$$\text{VSS}_q(\lambda, \theta) = -\text{VSS}_q(\lambda, 1 - \theta) \quad (7)$$

so rankings of demographic parameters and their complementary rates will be equal; optimists and pessimists need no longer disagree.

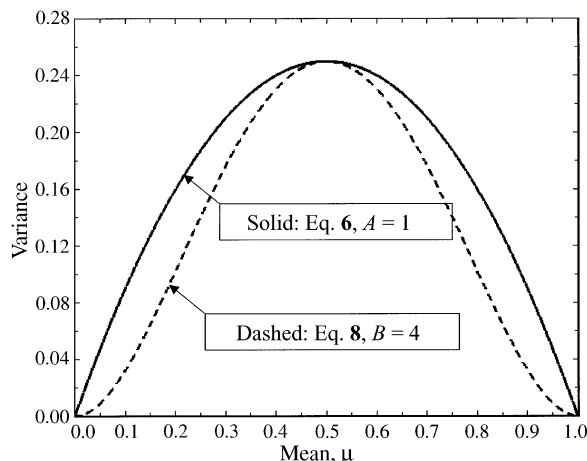


FIG. 1. Maximum variance as a function of expected value under two mean-variance relations. The solid line is  $\text{Var}(X) = A\mu(1 - \mu)$ , (Eq. 6) with  $A = 1$ ; the dashed line is  $\text{Var}(X) = B\mu^2(1 - \mu)^2$  (Eq. 8) with  $B = 4$ .

#### A DIFFICULTY—SPECIFICATION OF MEAN-VARIANCE RELATION

A difficulty with using variance-stabilized sensitivity is choosing the appropriate mean-variance relation. For  $\mu \in [0, 1]$ ,  $\mu^2(1 - \mu)^2 \leq \mu(1 - \mu)$ , so it is conceivable that the mean-variance relation for a demographic probability might be specified as

$$\text{Var}(\theta) = B\mu^2(1 - \mu)^2 \quad (8)$$

rather than by Eq. 6. A related variance-stabilizing transformation is based on the logit transformation,  $q(\mu) = \text{logit}(\mu) = \ln(\mu/(1 - \mu))$ . The variance-stabilized sensitivity based on the logit transformation satisfies Eq. 7: just as with,  $q(\mu) = \sin^{-1}(\sqrt{\mu})$ , optimists and pessimists can be in accord. How then does one choose between Eqs. 6 and 8, between arcsine-stabilized and logit-stabilized sensitivity?

The answer can only be that it depends on whether one believes Eq. 6 or Eq. 8 to be the correct description of the relevant mean-variance relation. It is noteworthy, however, that the range of admissible values for  $B$  depends on the value of  $\mu$ ;  $B\mu(1 - \mu)$  must not exceed 1, so that the largest possible uniformly acceptable value for  $B$  is 4 (Fig. 1). The specification  $0 \leq B \leq 4$  is unnecessarily restrictive when  $\mu$  is close to 0 or 1, and might only be justified on questionable retrospective grounds.

While it may be difficult to choose between Eq. 6 and Eq. 8, it ought generally to be easy to rule out inappropriate mean-variance relations. Thus, for instance, mean-variance relations for demographic probabilities that do not lead to variance-stabilized sensitivities satisfying Eq. 7 may be confidently dismissed. We suggest as well that in application to demographic parameters, the use of Eq. 8 rather than Eq. 6 would likely be justifiable only on retrospective grounds,



making Eq. 6 the more appealing option for prospective analyses.

#### ANOTHER DIFFICULTY—SCALING THE VARIANCE-STABILIZING TRANSFORMATION

Another difficulty with using variance stabilization as the basis of scaling for sensitivity analysis is that, even having chosen a specific general formulation for the mean–variance relation of a parameter, the variance-stabilizing transformation is not uniquely determined. Using, for instance, Eq. 6 as descriptive of the mean–variance relation, we observed that  $q(\mu) = \sin^{-1}(\sqrt{\mu})$  is a variance-stabilizing transformation, with  $\text{Var}(q(\theta)) \approx A/4$ . Clearly, any scalar multiple of  $q(\mu)$  is also variance stabilizing. From Eq. 4, it is easily seen that if,  $q_2(\mu) = cq_1(\mu)$ , where  $c$  is a scalar, the scaled sensitivity measures will differ by a multiplicative factor of  $c$ . Which value of  $c$  should be used?

If all of the demographic parameters under consideration were probabilities, all with mean–variance relation given by Eq. 6, it could be argued that the choice would not matter, so long as the same transformation were applied to all. The variances of the transformed variables would be qualitatively equivalent.

If some demographic probabilities were to be arcsine square-root transformed, while others were to be logit transformed, it seems sensible to multiply the former by 2, and the latter by  $\frac{1}{2}$ . Here is why: if  $\text{Var}(\theta) = A\mu(1 - \mu)$ ,  $\text{Var}(2 \sin^{-1}(\sqrt{\theta})) \approx A$ , where  $0 \leq A \leq 1$ . Under the mean–variance relation  $\text{Var}(\theta) = B\mu^2(1 - \mu)^2$ , with  $B$  bounded by 4 (its largest uniformly admissible value),  $\text{Var}(\frac{1}{2}\text{logit}(\theta)) \approx B/4 = A'$ , where  $0 \leq A' \leq 1$ . In both cases, the variance of the transformed parameter is approximately independent of the expected value of the parameter, and is interpretable as a proportion of the maximum attainable variance on the original scale.

However, suppose that some of the demographic parameters are probabilities, and others are fecundities, with mean–variance relation  $f(\mu) = k^2\mu^2$  leading to the log-transformation, and variance of  $k^2$  on the transformed scale. If it were possible to specify a maximum coefficient of variation,  $k_{\max}$ , for such fecundities, the transformation  $q(\theta) = \log(\theta)/k_{\max}$  would produce a new parameter with variance approximately independent of its expected value, again interpretable as a proportion of the maximum attainable variance on the original scale. This option might lose some of its appeal if the choice of  $k_{\max}$  is arbitrary.

These difficulties may be sidestepped by focusing on the components of fecundity that are probabilities (e.g., hatching success, percentage breeders, and fledging success) and comparing these probabilities, rather than fecundity itself, with other demographic probabilities of interest, applying the same transformation to all of the demographic probabilities. For some long-lived animals, the maximum individual fecundity is 1; the average number of offspring is then interpretable as a

probability, and thus directly comparable to other probabilities in the model. In the next section we more closely examine the killer whale example of Olesiuk et al. (1990) and Brault and Caswell (1993), in which this is the case.

#### KILLER WHALES AND VARIANCE-STABILIZED SENSITIVITY

Olesiuk et al. (1993) employed a two-sex, age-based population projection matrix model in examining the sensitivity of  $\lambda$  to a number of lower-level vital rates. Brault and Caswell (1993) used a stage-based population matrix model to address similar questions. Both models gave similar estimates of  $\lambda$  and reproductive values (Brault and Caswell 1993). However, as previously mentioned, Olesiuk et al. (1990) focused on mortality rates,  $\omega_i$ , in their sensitivity analyses, whereas Brault and Caswell (1993) focused on survival rates,  $\sigma_i$ , leading to different conclusions about which vital rates  $\lambda$  is most sensitive to.

Having noted that the inconsistent conclusions obtained by the two sets of authors are in fact artifacts of the use of elasticity for ranking the importance of demographic parameters, we decided to evaluate the demographic parameters these authors considered, using the variance-stabilized sensitivity (VSS) we have defined in this paper. We reconstructed the stage-based model of Brault and Caswell (1993; see Brault and Caswell for details) and calculated sensitivities, elasticities, and VSS for the lower-level parameters in each of these parameterizations; survival or mortality probabilities  $\sigma_i$  (or  $\omega_i = 1 - \sigma_i$ ), growth probabilities ( $\gamma_i$ ), and mean offspring production ( $m$ ). We treated calving as a Bernoulli trial; the probability of calving is essentially the same as the mean number of offspring since killer whales rarely produce twins. Thus we used the arcsine square-root VSS, i.e.,

$$\frac{\partial \log \lambda}{\partial [2 \sin^{-1}(\sqrt{\theta})]} = \left( \frac{\sqrt{\theta(1 - \theta)}}{\lambda} \right) \frac{\partial \lambda}{\partial \theta}$$

as a comparative measure of the importance of mean number of offspring, survival (or mortality), and growth rates.

Sensitivities to survival and mortality only differ by sign, whereas elasticities differ in magnitude (Table 1). It can clearly be seen why Brault and Caswell (1993) considered  $\lambda$  to be most sensitive to survival and Olesiuk et al. (1990) considered  $\lambda$  to be most sensitive to fertility ( $m$ ), thus leading to differing management recommendations. However, when using the arcsine VSS transformation, we conclude that  $\lambda$  is most sensitive (negatively) to changes in  $\gamma_3$  (−0.122), the rate at which whales leave the adult reproductive stage and enter the post-reproductive stage. The VSS of  $\lambda$  to fertility is a close second (0.115).

#### DISCUSSION

Comparisons of the sensitivity of  $\lambda$  to demographic parameters varying on different scales requires care;

TABLE 1. Sensitivities of the finite rate of population increase,  $\lambda$ , to lower-level vital rates for killer whales. Results are presented for the population matrix model of Brault and Caswell (1993).

Parameterized with survival, $\sigma$				Parameterized with mortality, $\omega$			
Parameter	Sensitivity	Elasticity	Arcsine VSS	Parameter	Sensitivity	Elasticity	Arcsine VSS
$\sigma_1$	0.0453	0.0422	0.0091	$\omega_1$	-0.0453	-0.0020	-0.0091
$\sigma_2$	0.3941	0.3785	0.0472	$\omega_2$	-0.3941	-0.0059	-0.0472
$\sigma_3$	0.5735	0.5585	0.0209	$\omega_3$	-0.5735	-0.0008	-0.0209
$\sigma_4$	0	0	0	$\omega_4$	0	0	0
$\gamma_2$	0.2062	0.0150	0.0529	$\gamma_2$	0.2062	0.0150	0.0529
$\gamma_3$	-0.5999	-0.0265	-0.1217	$\gamma_3$	-0.5999	-0.0265	-0.1217
$m$	0.3649	0.0422	0.1151	$m$	0.3649	0.0422	0.1151

Notes: The model is parameterized with survival ( $\sigma_{\text{stage}}$ ; Brault and Caswell 1993), as well as with mortality ( $\omega_{\text{stage}}$ ; sensu Olesiuk et al. 1990). Transition probabilities ( $\gamma_{\text{stage}}$ ) and mean offspring production ( $m$ ) are as defined in Brault and Caswell (1993). Log-scaled sensitivities differ with complementary rates (survival vs. mortality) while arcsine-scaled sensitivities do not.

the apparently contradictory conclusions of Brault and Caswell (1993) and Olesiuk et al. (1993) are merely artifacts of the definition of elasticity. We suggest that comparisons of the importance of demographic parameters require the selection of appropriate scales, and that these scales can be chosen by consideration of the demographic parameters as realizations of stochastic processes. We do not mean to blur the distinction between prospective and retrospective analyses by this suggestion; our recommendations are intended for prospective (functional) analyses of the effects on  $\lambda$  of demographic parameters. Our suggestion is that the functional relations taken into consideration ought to include functional relations between the mean and variance of the demographic parameters, regarded as stochastic processes. The functional relation between the mean and variance of any random variable distributed on the unit interval suggests that the arcsine square-root scale is appropriate for comparisons of demographic probabilities.

We agree with Nichols and Hines' (2002) and Heppell et al.'s (2000) views that focusing solely on elasticities for insight into management actions is not wise. Nichols and Hines (2002) suggest that elasticities ought to be considered in conjunction with the influence of management actions on parameters of interest, as well as the cost of such management actions in a decision-theoretic framework as a useful conceptual guide. They suggest a metric that, expressed in the notation of this paper, is

$$m(\theta) = \frac{\partial \log \lambda}{\partial \log \theta} \left( \frac{\partial \log \theta}{\partial x} \right) \frac{\partial x}{\partial y}$$

where  $\theta$  is a demographic parameter,  $x$  is a management action and  $y$  is the cost associated with the action. This metric, which reduces to proportional changes in  $\lambda$  per dollar spent, is especially attractive in that it not only focuses on realistic management actions and objectives, but also avoids the issue of scale: the relevant scale for management decisions may often be cost.

The utility of population matrix models in management and in addressing questions of evolutionary ecology has grown in recent years. We believe the use of appropriately scaled variance-stabilized sensitivities (VSS), as we have advocated here, will further advance such uses, while avoiding conclusions based on inappropriate scalings.

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## APPENDIX

### VARIANCE BOUNDS FOR RANDOM VARIABLES DISTRIBUTED ON THE UNIT INTERVAL

The relation  $0 \leq \text{Var}(X) \leq \mu(1 - \mu)$  for random variables  $X$  with distributions restricted to the interval  $[0, 1]$  is easily established. Clearly,  $X^2 \leq X$ , from which it follows that the expected value of  $X^2$  is less than the expected value of  $X$ . Subtracting the square of the expected value of  $X$  from both sides of the inequality, we have

$$E(X^2) - [E(X)]^2 \leq E(X) - [E(X)]^2$$

Recognizing the left-hand side of this equation as equivalent to  $\text{Var}(X)$ , which must be non-negative, and substituting  $\mu$  for  $E(X)$ , we obtain,  $0 \leq \text{Var}(X) \leq \mu - \mu^2$ , the desired result.